

## ARE MANGROVES NURSERY HABITAT FOR TRANSIENT FISHES AND DECAPODS?

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**Abstract:** The term nursery implies a special place for juvenile nekton (fishes and decapod crustaceans) where density, survival, and growth of juveniles and movement to adult habitat are enhanced over those in adjoining juvenile habitat types. We reviewed recent literature concerning these four topics and conducted meta-analyses for density and survival data. Most studies of mangroves as nurseries have addressed only occurrence or density of fishes or decapods, have not used quantitative sampling methods, and have not compared alternate habitats. Comparison of nekton densities among alternate habitats suggests that, at times, lower densities may be typical of mangroves when compared to seagrass, coral reef, marsh, and non-vegetated habitats. There is little direct consumption of mangrove detritus by nekton. C, N, and S isotope studies reveal little retention of mangrove production by higher consumers. Densities of prey for transient fishes and decapods may be greater within mangroves than elsewhere, but there has been no verification that food availability affects growth or survival. Experimental evidence indicates that mangrove roots and debris provide refuge for small nekton from predators, thus enhancing overall survival. There is no evidence that more individuals move to adult habitats from mangroves than from alternate inshore habitats. There is an obvious need to devise appropriate experiments to test the nursery functions of mangroves. Such data may then be one more reason to add support for mangrove conservation and preservation.

**Key Words:** mangroves, nursery, fishes, decapods, habitat, estuary, coastal zone, conservation, meta-analysis

### INTRODUCTION

Mangrove forests dominate the low-energy intertidal zones of river deltas, lagoons, estuaries, and coastal systems in the tropics, subtropics, and along some temperate coasts (Twilley et al. 1996). Mangroves have been widely assumed to provide nursery habitat functions for juvenile fishes and decapods and to support local fisheries, similar to functions ascribed to salt marshes. Several studies have noted positive relationships between mangrove area and local fishery production (for example, Martosubroto and Naamin 1977, Yáñez-Arancibia et al. 1985b, Turner 1992, de Graaf and Xuan 1998). Mangroves have also been shown to

export dissolved and particulate materials into the coastal zone (Alongi 1989, Hatcher et al. 1989, Chong et al. 1990, Lee 1995). These materials are thought to stimulate coastal productivity, as indicated by appreciably greater fishery yields off coasts with estuarine mangrove forests than off non-mangrove coasts (Marshall 1994). In addition, mangroves are believed to provide the same food, shelter, and refuge functions that have been ascribed to other vegetated intertidal and subtidal habitats (Odum et al. 1982, Blaber 1986, Robertson and Blaber 1992). The importance of mangroves as nurseries has been one of the reasons advanced to support the conservation and management of mangroves and to stem their rapid loss. Many coun-

tries in Africa, Latin America, and Asia are now estimated to have lost at least 50% of their original mangrove area (Burke et al. 2001).

There have been warnings, however, that supportive data have not been collected and that fish and decapod use of mangroves may not be the same in all areas of the globe (Chong et al. 1990, Hoss and Thayer 1993). Even the mechanisms of use of mangrove detritus by inshore and offshore consumers are largely unknown (Lee 1995). For example, mangrove leaf processing by crab herbivores within forests is high in northeast Queensland and low in southwest Florida, suggesting that the transfer of mangrove primary production to higher consumers varies spatially and temporally (McIvor and Smith 1995). Mangrove detritus, however, seems to be of little nutritional significance once it leaves the forest (Rodelli et al. 1984, Hatcher et al. 1989, Fleming et al. 1990, Manguillier et al. 1997).

In this review, we examine the scientific basis for suggesting that mangroves are critical nursery habitat for transient fishes and decapods. Many of these nekton species are economically important. The concept of coastal habitats as nurseries for juvenile fishes and decapods is pervasive, yet it has rarely been stated clearly or even tested (Heck et al. 1997, Beck et al. 2001). Thayer et al. (1978) proposed that "To be of significance as a nursery . . . , a habitat must provide adequate protection from predators, . . . , or a food source which is both varied and concentrated." The terms "adequate," "varied," and "concentrated" are all vague, though, and do not describe someplace special where functions and processes should be enhanced over those in adjoining habitats. Dennis (1992) began to address functional differences among habitats when he defined a nursery as an area with low predation or starvation rates. For the purposes of this review, we follow the definition of a nursery habitat provided by Beck et al. (2001): "A habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur. The ecological processes operating in nursery habitats, as compared to other habitats, must support greater contributions to adult recruitment from any combination of four factors: (i) density, (ii) growth, and (iii) survival of juveniles, and (iv) movement to adult habitats." We also follow Dennis (1992) in defining mangrove habitat as the prop root or pneumatophore system and adjacent lagoons, creeks, and pools that are derived from mangrove-induced deposition processes.

## METHODS

We conducted a survey of the recent literature compiled by Aquatic Sciences and Fisheries Abstracts

(Cambridge Scientific Abstracts; <http://www.csa.com/>) for the period 1980–2000 using the keyword combinations of 1) mangrove and 2) fish, fisheries, decapod, crab, shrimp, prawn, or nursery. From this collection of articles plus our personal libraries, we reviewed 312 relevant publications in major international journals, many regional journals, and several books that dealt with density, feeding, growth, survival, or movement of fishes or decapods.

To be considered for further analysis, studies had to employ quantitative methods and to compare mangroves with typical adjacent habitats such as seagrass beds, coral reefs, marshes, or non-vegetated sands or muds. Only 32 studies met one or both of these criteria (see following section). Enclosure traps, block nets, metered plankton nets, or visual census with defined areas or volumes are required for density estimates (Bortone et al. 1989, Rozas and Minello 1997). Popular sampling gears such as gill nets, seines, and trawls are termed qualitative, and results from studies employing them were avoided for several reasons: these gears are usually pulled adjacent to (not within) mangrove root zones because they are ineffective in most types of vegetation; catch efficiencies are low and variable; recovery efficiencies are hard to measure; sample area can be difficult to define; and gear avoidance can be high (Rozas and Minello 1997). Another popular sampling method, using a net to block off a section of mangrove forest in order to catch nekton moving out with the falling tide, is only quantitative when lateral and inward movement is prevented and the sampling area is measured. Estimates of growth, survival, and movement success need to employ appropriate mensurative or manipulative experiments (Hurlbert 1984). Finally, each species studied has to have a life history consistent with the nursery role hypothesis (i.e., some spatial disjunction between juvenile and adult habitats) (Beck et al. 2001).

We compiled information for meta-analysis by extracting data from studies examining mangroves and at least one different habitat type (such as seagrasses, non-vegetated bottom, or coral) that were reported in such a way that means, standard deviations, and sample sizes could be determined. Some data were estimated from error bars in figures if tabular data were not presented. We used all appropriate species in a given study even if some habitat densities were zero. We conducted meta-analyses only of density and survival data, as growth and movement were limited to one study each (Dittel et al. 1997 and Costello and Allen 1966, respectively). Few studies reported nekton size data in enough detail for useful comparisons. If a study reported separate survival or density data on multiple (appropriate) species, these data were considered independent and were included as separate lines

of data in the meta-analysis. Aggregate data that lumped appropriate species with mangrove residents (e.g., "total fish abundance") were excluded. For studies that reported density data with temporal replication (e.g., Sheridan 1992), data for each species were pooled and new means and standard deviations were calculated if it was unclear whether or not these samples represented independent cohorts.

We employed Hedges'  $d$  (Hedges and Olkin 1985) for our meta-analysis metric. Hedges'  $d$  accounts for the effects of small sample sizes and is calculated as

$$d = \frac{(\bar{X}^e - \bar{X}^c)}{S} J,$$

where  $S$  is the pooled standard deviation and  $J$  is

$$J = 1 - \frac{3}{4(N^c + N^e - 2) - 1}.$$

Therefore,  $d$  describes the difference between experimental (in this case, mangrove) and control groups in terms of standard deviation units. A positive value of  $d$  in our analysis would reflect greater abundance or survival of species in mangrove habitats than elsewhere.

All calculations and analyses were conducted using MetaWin 2.0 (Rosenberg et al. 2000). Hedges'  $d$  was calculated for each line of data collected above, then a weighted mean effect size for survival and for density across all studies was determined. Confidence intervals for the mean effect sizes were generated using bootstrapping methods and were used to test mean effect sizes for significant differences from zero with  $\alpha = 0.05$ . Confidence intervals generated through randomization techniques are considered more conservative than parametric methods, and there is no underlying assumption about normality of the data (Rosenberg et al. 2000). However, percentile bootstrap confidence intervals do assume that the distribution of bootstrapped values is centered around the original mean value; therefore, we used bias-corrected bootstrap confidence intervals to ameliorate any bias that could arise due to the small sample sizes reported in the studies used (Efron 1987, Rosenberg et al. 2000).

In addition to estimating the mean effect size across studies, it is useful to determine whether the variance among effect sizes calculated for individual studies is greater than one would expect through sampling error alone. The total heterogeneity of a sample, or  $Q_i$ , can be calculated as

$$Q_i = \sum_{i=1}^n w_i(E_i - \bar{E})^2,$$

where  $E_i$  is the effect size for the  $i^{\text{th}}$  study, and  $w_i$  is the reciprocal of its sampling variance.  $Q_i$  is a weight-

ed sums of squares and, as such, is analogous to the total sums of squares in an analysis of variance (Rosenberg et al. 2000). A significant  $Q_i$  indicates that there may be some underlying structure to the data. In addition to the "no structure" meta-analytical model, it is possible to address variation in mean effect size in studies that vary either due to a categorical variable (e.g., species of mangrove) or a continuous variable (e.g., latitude at which the study was conducted). Categorical meta-analysis was performed only on density data due to the limited number of survival, growth, and movement publications. Within the density data, we examined the effect of differing alternate habitat types (coral, seagrass, and non-vegetated, the latter comprising lagoon, open bay, marsh-lined river, sand and mud bottoms, or bare experimental traps).

## RESULTS OF LITERATURE REVIEW

### Mangrove Nekton Densities

A recent review of mangrove ecosystems (Kathiresan and Bingham 2001) concluded that there was ample evidence that juvenile shrimps, prawns, crabs, and fishes used mangrove habitats as nurseries due to greater densities there than elsewhere. Close inspection of the literature citations employed to support their statements reveals that, among other inconsistencies, those studies either examined only mangrove habitat, used the same qualitative sampling gear in two or more habitat types, or used different qualitative sampling gears in differing habitat types (e.g., Chong et al. 1990, Sasekumar et al. 1992, Sedberry and Carter 1993, Pinto and Punchihewa 1996, Acosta 1997, Laroche et al. 1997, Tzeng and Wang 1997). Several other widely cited reports that proclaim mangroves as nurseries suffer from the same problems (e.g., Robertson and Duke 1987, Laegdsgaard and Johnson 1995).

Most of the 32 articles that we list in Table 1 used quantitative sampling methods and employed the term nursery positively in conjunction with mangroves, supporting the worldwide perception that mangroves are nursery habitats for transient nekton. Both Rooker and Dennis (1991) and Ley et al. (1999) specifically noted that sub-adult transients were common in mangroves but juveniles were not and that nursery functions were limited to high salinity areas. Rajendran and Kathiresan (1999) discussed high densities of juveniles but not in the context of nurseries. Sheridan (1992), Mullin (1995), and Lorenz et al. (1997) discussed neither life history stages nor nursery functions of habitat types. Collins and Finucane (1984) named waters seaward of mangrove habitats as nurseries but did not apply the term to mangrove creeks and waterways. It is apparent, however, that there are several shortcomings even

Table 1. Summary of research on juvenile fish and decapod use of mangroves and alternate habitats. Nursery = yes if mangroves were termed nurseries in text; = no if mangroves were directly or by omission named as non-nurseries; = maybe if nursery function depended on other variables such as salinity, if sub-adults but not juveniles were linked to mangroves, or if mangroves were described as habitats with heightened density, growth, development, survival, or refuge for young but were not directly termed nurseries; = n/a if nursery roles were not addressed. Taxa examined: C = crabs, F = fishes, L = lobsters, S = shrimps. Habitat types compared: c = coral, e = emergent marsh, m = mangroves, n = non-vegetated mud or sand, s = seagrass. The term "block net" encompasses several types of gear that block exit of nekton from a sampling site. Quantitative = yes, if method used provided quantitative information, or — if not quantitative or uncertain.

Authors	Year	Location	Nursery	Taxa	Habitat		Method of Data Collection		
					Types	Factor Addressed	Gear Type	Quantitative	
Acosta	1999	Belize	yes	L	mc	density	visual census	yes	
Acosta and Butler	1997	Belize	yes	L	msc	survival	tethering experiment	yes	
Bell et al.	1984	New South Wales	yes	F	m	density	block net	—	
Blaber and Milton	1990	Solomon Islands	yes	F	m	density	block net	yes	
Boulon	1992	Virgin Islands	yes	F	m	density	visual census	yes	
Browder et al.	1986	Florida	yes	CFS	m	density	plankton net	yes	
Collins and Finucane	1984	Florida	no	F	m	density	plankton net	yes	
Costello and Allen	1966	Florida	yes	S	ms	movement	tagging experiment	—	
Dennis	1992	Puerto Rico	yes	F	msc	density	plankton net	yes	
Dittel et al.	1997	Costa Rica	yes	S	m	growth	feeding experiment	yes	
Halliday and Young	1996	Queensland	yes	F	m	density	block net	yes	
Kuo et al.	1999	Taiwan	yes	F	m	density	block net	—	
Ley et al.	1999	Florida	maybe	F	m	density	block net, visual census	yes	
Lin and Beal	1995	Florida	yes	CFS	m	density	block net	yes	
Lin and Shao	1999	Taiwan	yes	F	m	density	block net	yes	
Little et al.	1988	Kenya	yes	F	m	density	plankton net	yes	
Lorenz et al.	1997	Florida	n/a	F	m	density	block net	yes	
Morton	1990	Queensland	yes	F	mns	density	block net	yes	
Mullin	1995	Florida	n/a	F	ms	density	block net	yes	
Nagelkerken et al.	2000	Bonaire	yes	F	mcs	density	visual census	yes	
Peebles and Flannery	1992	Florida	yes	F	men	density	plankton net	yes	
Primavera	1997	Philippines	yes	S	mn	survival	predation experiment	yes	
Rajendran and Kathiresan	1999	India	maybe	CFS	m	density	manipulative experiment	yes	
Robertson	1988	Queensland	yes	S	m	density	block net	—	
Robertson and Duke	1990	Queensland	yes	F	m	density	block net	—	
Rönnbäck et al.	1999	Philippines	yes	FS	m	density	block net	yes	
Rooker and Dennis	1991	Puerto Rico	maybe	F	m	density	visual census	yes	
Rooker et al.	1996	Puerto Rico	yes	F	mcs	density	plankton net	yes	
Sheridan	1992	Florida	n/a	CFS	mms	density	drop trap	yes	
Thayer et al.	1987	Florida	yes	F	m	density	block net	yes	
Vance et al.	1996	Queensland	yes	FS	m	density	block net	yes	
Wright	1986	Nigeria	yes	F	m	density	block net	yes	



within this quantitative database. First, comparative habitat data are relatively rare, as 21 of the 32 studies examined nekton use of mangrove habitats only. Within those 21 studies, there were four block net studies that we considered qualitative: two because they did not report the area fished (Bell et al. 1984, Kuo et al. 1999) and two because it was unclear whether the surveyed areas had physical obstacles that prevented lateral movement out of the sites since enclosure nets did not completely block the areas fished (Robertson 1988, Robertson and Duke 1990). Two other studies examined nekton densities in adjoining mangrove habitat types but no non-mangrove habitats (Vance et al. 1996, Rönnbäck et al. 1999).

There were seven studies that compared densities in mangroves versus adjacent habitats (Table 1). Three studies employed plankton nets towed at night to estimate densities of larval and postlarval fishes. Peebles and Flannery (1992) reported densities of fishes along a transect from open bay to headwaters of a river, the lower reaches of which were lined by mangroves and the upper reaches by marshes. Comparison of mangrove-lined river to marsh-lined river and to open bay revealed no differences in overall (2-year) average densities of transient fishes. Dennis (1992) and Rooker et al. (1996) employed a plankton net/night light combination that sampled a fixed volume of the water column to estimate larval fish densities adjacent to mangrove prop roots, coral reef, sand bottom, or lagoon habitats. Both studies indicated lower fish densities near mangroves than elsewhere. The remaining four studies examined nekton densities in different ways. Acosta (1999) employed visual censusing techniques to estimate densities of juvenile spiny lobster *Panulirus argus* (Latreille, 1804) around mangrove islands versus coral islands without mangroves. He found no difference in spiny lobster densities, although density values were not given. Nagelkerken et al. (2000) used visual censusing techniques to compare reef fish densities in mangrove, seagrass, and shallow (< 3 m deep) coral habitats. Juveniles of nine of 14 fish species had greater densities near mangroves than over seagrasses or shallow coral reefs. Nagelkerken et al. (2000) also provided data for three deeper (> 3 m) coral reef habitats, but juveniles were rarely found there so we excluded those data. Rajendran and Kathiresan (1999) experimentally examined the role of mangrove leaves as attractants by baiting intertidal traps with mesh bags containing or not containing mangrove leaves. Seasonal mean nekton densities were usually greater in mangrove traps than in structure-only traps, indicating that some aspect of the decomposition of mangrove debris served as a faunal attractant. Sheridan (1992) employed a 2.6 m<sup>2</sup> drop trap to compare seasonal densities of fishes and decapods just inside the edge of a

flooded mangrove forest and a short distance seaward over seagrasses or non-vegetated mud substrata. The majority of dominant species either showed no difference in densities or lower densities within mangroves (including several economically important species), and total fish and decapod densities (minus dominants) were always lower within mangroves. The available data suggest that nekton densities are not consistently enhanced in mangroves relative to other habitat types. These results may be regionally biased since only one of the studies (Rajendran and Kathiresan 1999) was conducted outside of the Gulf of Mexico–Caribbean area.

Although many biotic and abiotic factors can affect density estimates, tidal stage is a critical factor that needs to be included in any sampling design attempting to compare intertidal habitats to subtidal habitats. In the aforementioned studies, Peebles and Flannery (1992) and Sheridan (1992) sampled nekton during flood tides so that organisms could access any available habitat type. Rajendran and Kathiresan (1999) sampled intertidal traps at low tide after organisms had access to all traps. Moon phase was controlled by Dennis (1992, new moon only) and Rooker et al. (1996, quarterly moon phases), but tidal stage was not mentioned. Neither tidal stage nor moon phase was mentioned by Acosta (1999) or Nagelkerken et al. (2000), although they did indicate that work was conducted in microtidal environments. Future quantitative density comparisons need to be made when organisms have equal access to flooded intertidal and subtidal habitats.

#### Habitat Functions of Mangroves for Nekton

We found only four mensurative or manipulative experiments addressing the questions of whether growth is faster, survival is greater, or movement to adult habitat is more successful for transient juveniles using mangrove habitats than for those using adjacent habitats (Table 1: Costello and Allen 1966, Acosta and Butler 1997, Dittel et al. 1997, Primavera 1997). These studies are discussed within the broader background of how mangroves might function for juvenile nekton.

The single study relevant to growth in mangrove habitats was a series of short-term (6-day) experiments by Dittel et al. (1997: Figure 1b). Their results indicated that postlarval whiteleg shrimp *Litopenaeus vannamei* (Boone, 1931) (previously *Penaeus vannamei*, Farfante and Kensley 1997) grew more rapidly on a diet of mangrove detritus mixed with zooplankton and meiofauna than on a diet that was primarily mangrove detritus with little meiofauna. Unfortunately, this laboratory study did not place the shrimp in any particular habitat, but it does indicate that mangrove detritus *per se* is a low quality food.

Organism growth in a given habitat is affected by quality, quantity, availability, and assimilation of food. There was little evidence that juvenile fishes or decapods directly consume mangrove debris or detritus, which is relatively refractory material (Austin and Austin 1971, Odum and Heald 1972, Fagade and Olaniran 1973, Beumer 1978, Kinch 1979, Marte 1980, Robertson 1988, Salini et al. 1990, Thollot et al. 1999; exceptions noted by Cannicci et al. 1996, Pinto and Punctihewa 1996). Assimilation of mangrove organic matter, as indicated by stable C, N, and S isotope signatures, also appears to be minimal. To date, food materials assimilated within mangrove ecosystems have usually been derived from algae, seagrasses, or water-column particulates (Stoner and Zimmerman 1988, Harrigan et al. 1989, Szelistowski 1990, Primavera 1996, Loneragan et al. 1997, Marguillier et al. 1997, Mohan et al. 1997) and rarely from mangroves (Rodelli et al. 1984). There are indications that the isotopic signatures of mangrove organic matter may be found only in organisms caught immediately adjacent to or within mangrove forests, compared to offshore specimens of the same species (Rodelli et al. 1984, Fleming et al. 1990, Newell et al. 1995, Mohan et al. 1997). Both Zieman et al. (1984) and Fry et al. (1987) indicated that pink shrimp *Farfantepenaeus duorarum* (Burkenroad, 1939) (previously *Penaeus duorarum*, Farfante and Kensley 1997) from mangrove creeks had carbon isotope signatures closer to those of mangroves than did pink shrimp from seagrass beds, even though capture sites were < 1 km apart. This finding suggests that the isotopic signatures of transient nekton moving in and out of mangrove habitats could vary with the time spent foraging in a particular habitat. Fry et al. (1999) indicated that tissue turnover in rapidly growing juvenile penaeid shrimps may influence food source signals within days to weeks. The nutritional value of mangroves for transient nekton is thus linked to limited tidally-mediated availability of mangrove habitat, which may not be detected with limited field sampling. To our knowledge, there has been no experimental verification that foods available within mangrove habitats, whatever their isotopic signatures, provide for faster growth than foods available in adjacent habitats.

Experimental evidence provided by Primavera (1997) indicated that the presence of debris or sediments did not provide refuge for penaeid shrimps, but mangrove pneumatophores at moderate densities did prevent predation by some predatory fish species. Acosta and Butler (1997) found that survival of tethered spiny lobster was greater in mangrove prop roots than in seagrass or coral. Vance et al. (1996) noted that mangrove prop roots prevented large predatory fishes from penetrating distances beyond 26 m into the

flooded forest, while penaeid shrimps and smaller fishes were collected up to 43 m into the forest. Thus, there is some evidence that mangrove roots increase survival by providing refuge from predators.

A variety of studies have linked juvenile nekton in mangroves with adult populations elsewhere (for example, Yáñez-Arancibia et al. 1985a, Blaber et al. 1989, and Parrish 1989; but see Robertson and Blaber 1992 for an opposing view). Few experimental studies have actually marked organisms in one habitat and recaptured them in another or used naturally occurring marks (such as otolith chemical constituents, e.g., Gillanders and Kingsford 1996) to identify sources of organisms on adult habitats (see Gillanders et al. 2003). We located only one study comparing success of movement from mangrove and alternate habitats. Costello and Allen (1966: Table 1) released tagged juvenile pink shrimp in both mangrove lagoons and seagrass beds, then noted their recapture rates by the offshore shrimp fishery. There was no difference in overall recapture rates, perhaps indicating equal success in movement from both habitats. A more recent study that did not use individually marked organisms was conducted by Fry et al. (1999). They used stable C and N isotopes to determine that the source of new recruits to the offshore pink shrimp fishery was primarily from organisms assimilating seagrasses, not mangroves. If pink shrimp movement is relatively slow, then isotope ratios would be expected to change as shrimp move from coastal mangroves through seagrasses or other habitat types to offshore adult habitats. If pink shrimp move rapidly and retain their juvenile isotopic signatures, then these results would indicate relatively poor movement success from mangrove habitats. As yet, there have been no experiments to test whether juvenile fishes or other decapods living in mangrove habitats survive in greater proportion while moving to adult habitats than those living elsewhere.

#### Meta-analysis of Mangroves as Nurseries

A mixed-effects model was used to test density data for different mean effect sizes with different non-mangrove habitat types. Appropriate data were extracted from Dennis (1992: Table 1), Peebles and Flannery (1992: Table 9), Sheridan (1992: Tables 2–5), Rooker et al. (1996: Table 1, Ahogado only), Rajendran and Kathiresan (1999: Figure 1b), and Nagelkerken et al. (2000: Table 2). Although Acosta (1999) addressed density, no relevant data were provided since no density differences were noted between mangrove islands and coral islands. The mean effect size  $d$  was negative ( $-4.637$ ) and was significantly different from zero (95% CI =  $-9.936$  to  $-0.930$ ; Table 2) using re-sampling methods; thus, densities in mangroves appeared

Table 2. Results of meta-analyses of density and survival of fishes and decapods in mangroves and alternate habitat types using Hedges' *d* and non-parametric variances. Resampling tests generated from 999 iterations. *Q* = heterogeneity. Confidence intervals (CI) are bias-corrected. Mean effect size is significant if CI does not overlap zero.

Data Type	Analysis Type	Q	df	P	Estimated Pooled Variance	Mean Study Variance	Mean Effect Size	95% CI
Density	Summary results (random effects model)	42.789	113	1.000	1532.396	0.134	-4.637	-9.936 to -0.930
	Categorical results							
	Unvegetated (n = 50)				1854.852		-3.483	-12.031 to 1.463
	Coral (n = 21)				1394.819		-11.291	-27.842 to 2.453
	Seagrass (n = 43)				297.815		-2.730	-8.260 to 1.460
Survival	Model							
	Between	0.752	2	0.686				
	Within	42.037	111	1.000				
	Total	42.789	113					
	Summary results (random effects model)	7.157	7	0.413	0.225	0.750	0.839	0.180 to 1.421

to be lower than in coral, seagrass, and non-vegetated bottom habitats as a group. However, the model detected no significant effect of any single non-mangrove habitat type since the categorical mean effect sizes for each non-mangrove habitat were not significantly different from zero. We note here that the limited number of relevant studies yielded a relatively small data base for meta-analysis (114 between-habitat comparisons, Table 2) and that only one study was conducted outside of the Gulf of Mexico–Caribbean region. Our results must then be considered preliminary until further data become available.

The mean effect size calculated from the survivorship data [Acosta and Butler (1997: Figure 3) and Primavera (1997: Figures 1b, 2b)] was positive and significant (0.839; 95% CI = 0.180 to 1.421; Table 2), indicating that survival of the species studied was greater in mangrove habitat than in non-mangrove habitat. However, the data set was extremely limited (8 between-habitat comparisons), and these results must be considered preliminary.

## DISCUSSION

Beck et al. (2001) proposed that the term nursery implies a special place for juvenile marine organisms where functions and processes such as density, survival, growth, and movement to adult habitat are enhanced over those in adjoining habitat types. Prior to this review, three hypotheses had been advanced to explain the seemingly large densities of nekton in, and the apparent dependence of certain species upon, mangrove coastlines (Robertson and Blaber 1992). These hypotheses fit into the framework developed by Beck et al. (2001). One hypothesis stated that mangroves provide greater food densities and thus permit faster growth than adjacent habitats. In Queensland, greater densities of planktonic crab larvae have been found within mangrove prop roots than over adjacent seagrasses or mud flats during some seasons, and these crab larvae are actively selected by predatory fishes (Robertson et al. 1988). In Florida, benthic faunal densities within prop root habitat were greater than densities in adjoining seagrasses and mud banks (although biomass was not; Sheridan 1997). However, experimental verification that these greater prey densities provide for faster growth of fishes and decapods is lacking. A second hypothesis was that turbid waters (which are typical of all estuaries, not just mangrove estuaries) reduce the effectiveness of predators. This has been tested and found true for some predatory species, but not for others, in several types of estuaries (Grechay and Targett 1996, Primavera 1997, and references therein). The third hypothesis stated that the structural complexity of mangrove roots reduces pred-

ator efficiency, as does structure in other vegetated habitats. Again, there is some evidence for this function. Tethered spiny lobsters experience greater survival in mangrove prop roots than in seagrass or coral habitats (Acosta and Butler 1997). Reduction of predator effectiveness by mangrove structure, however, is likely to be predator-specific and thus is not a universal benefit (Primavera 1997). The final component of the nursery role hypothesis developed by Beck et al. (2001), that the journey from mangrove nurseries to adult habitats is somehow more successful than from other habitats, has not been addressed experimentally.

There is an obvious need to devise appropriate quantitative field and laboratory experiments to test the nursery functions of mangroves. The two simplest types of data to collect (presence and density) are the least helpful in defining whether any habitat is a nursery habitat. The nursery value of mangroves and other intertidal habitats is controlled by limited tidally-mediated access, which must be factored into interpretations of habitat value. *In situ* studies of growth and survival across the various mangrove ecosystem habitats, and in comparison to adjacent habitat types such as emergent marshes, seagrasses, non-vegetated flats, and coral reefs, are required. The process of movement from juvenile to adult habitat and its results also need thorough investigation. Until these data are gathered, the case for identifying flooded mangrove forests as critical nursery habitat for transient fishes and decapods remains equivocal.

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